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Vol. 4, No. 10, pp. 159-176, pls. 21-24 March 8, 1911

ERYTHROPHYLLUM DELESSERIOIDES J. A.G.

BY

WILFRED CHARLES TWISS

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ERYTHROPHYLLUM DELESSERIOIDES J. AG.*

BY

WILFRED CHARLES TWISS.

Erythrophyllum delesserioides, a member of the Rhodophyceae inhabiting the litoral and sublitoral zones of the California coast, has been a cause of some difference of opinion among algologists, relative to its position in the group.

The plant was first described by J. G. Agardh (cf. 1871, p. 10), who came into possession of a young sterile specimen from the herbarium of J. E. Gray. Agardh recognized in it a striking form, and, on the basis of its vegetative structure assigned it to Gigartinaceae, with possible close relationship to Callophyllis. In 1879 (cf. p. 173, pl. 15, figs. 1-3) he published illustrations from the specimens in his possession.

Schmitz, who had also examined only sterile specimens, afterwards defined its position as doubtful, though he expressed the opinion that its probable place was among Dumontiaceae, rather than with Gigartinaceae (cf. 1897, p. 521).

As to the specimens distributed, very young plants were first sent out by F. S. Collins in 1894 (cf. Hauck and Richter's Phyk. Univ., Fasc. XIII, under No. 606). The following year Mrs. J. M. Weeks distributed young plants (cf. Collins, Holden and Setchell's Phyc. Bor.-Am., Fasc. I, under No. 50). In 1899 Setchell and Gibbs distributed, for the first time, mature plants,

* A thesis submitted in partial satisfaction of the requirements for the degree of Master of Arts, University of California, May, 1910, but since amplified.

upon which fruiting proliferations were formed (cf. Phyc. Bor.-Am., Fasc. XII, under No. 588). Here the cystocarps were first mentioned by Setchell, with the statement that they were Gigartinaceous in character and that the genus should, therefore, remain with Gigartinaceae, where Agardh had placed it, and not in Dumontiaceae, as suggested by Schmitz. The last distribution was by Josephine E. Tilden, who, in 1902, sent out young plants (cf. Am. Algae, under No. 505).

In 1899 Agardh published a more complete description of the sterile form which he had examined, amplifying his former statements, and reaffirming his belief in the correctness of his first classification. He then referred to the mature plant that had been distributed by Setchell and Gibbs as probably of a different genus, and proposed for it the name *Polyneura californica* (cf. 1899, p. 57). As will be seen by reference to the illustrations presented herewith and to the specimens distributed as above mentioned, there is such a marked difference between the young and the mature plants that Agardh's disbelief in their identity seems somewhat justifiable (cf. Setchell and Gardner, 1903, p. 303; also, De Toni, 1895, p. 1639).

Although Setchell possesed a complete series of plants in different stages, establishing beyond a doubt the fact that the youthful and mature forms which had been distributed belonged to one and the same species, he nevertheless, in 1903, examined the specimens in Agardh's herbarium, in order to satisfy himself concerning the exact nature of the material which the latter had used in his studies. Setchell's notes are as follows:

> "*Erythrophyllum delesserioides.*
>
> No. 25374 (type and only specimen) upper portion (dimidium) from the herbarium of J. E. Gray, Vancouver Island. Characteristic young plant. See tracing.
>
> *Polyneura californica.*
>
> No. 25375 (3 specimens).
>
> Plant from Mrs. Hall, older, much split and the papillae just showing.
>
> No. 25376. Plant from Eaton (no. 73), much eroded, with papillae.
>
> No. 25377. A bit from P. B.-A.—Later specimen *Erythrophyllum delesserioides.*"

Fig. 1 (plate 21) is a reproduction of Setchell's tracing, referred to above. Fig. 2 was drawn from a specimen similar to Agardh's older forms.

As yet, however, no careful study had been made of the structure of the fruiting proliferations, their vegetative characteristics chiefly having been taken into consideration in the previous assignments of the plant to Gigartinaceae and Dumontiaceae, respectively. Such being the state of the case, it was suggested by Professor Setchell that an investigation of the structure and development of the papillae, and more especially of the cystocarp, would be advisable, in order to establish the position of the plant more definitely. For the pursuance of this object the publications, notes, etc., above referred to, were made available, together with the collections and preserved material of the University of California.

As previously stated, *Erythrophyllum delesserioides* is an inhabitant of the litoral and sublitoral zones of the western coast of North America, of California in particular, and extending as far north as Vancouver Island, B. C. The young plant possesses a delicate leaf-life thallus, somewhat oval in outline with a slight mid-rib-like thickening along the median line. The apex of the thallus blade is rounded and the blade more or less truncate, with or without a short stipe connecting it with a discoid holdfast. The margin is wavy, generally more or less incised by an oblique splitting toward the base and toward the median line. The color of the plant, in its natural habitat, is brick red, changing to a dark ruby hue in the preserved material. The consistency is firm gelatinous, but not hard or horny, as in the case of *Gigartina mamillosa*, for instance. The proportions found in a moderately young plant were as follows: length, 5 cm.; width, 2 cm.; stipe, 5 cm. An older plant had a length of 18 cm. and a width of 4.5 cm., was greatly incised along the margin, and showed a much stronger development of the mid-rib-like thickening of the median line than was found in the young plant. A few incipient branches of the mid-rib had been developed, which, proceeding toward the margin and projecting forward and outward at an acute angle, served as supports for the lobes formed by the in-

cisions above mentioned. These lateral lobes are often themselves incised, and their ribs branched, as in the case of the main rib. In older specimens dichotomous branching of the main rib may occur. Often a number of separate blades were found, originating at or near the holdfast, or, where the stipe was elongated, at a distance of 5 cm. or more from the point of attachment. The above measurements are intended merely to indicate the proportions found in growing plants. A much larger growth is eventually attained, some of the specimens at hand having a length of 30 cm. or more.

As the season advances, the incisions increase in number and the edges of the thallus blades become more or less worn away, so that by the time the papillae are fully developed, the plant has assumed a somewhat attenuated appearance with a comparatively narrow, truncated blade, and a much greater proportional development of stipe, mid-rib and lateral branches.

The final stage, as seen in specimens gathered in January, consists of scarcely more than the mid-rib and its lateral branches which are still covered, and that, too, very densely, with papillae.

The papillae, to be described more particularly later, are minute proliferations, somewhat rounded terminally in the case of the cystocarpic, and elongated or thumb-shaped, in that of the tetrasporic. Antheridial plants have not yet been observed.

During the following spring the plants are broken or worn down to mere fragments, attached to the rocks by their holdfasts. As summer advances, these fragmentary stipes may send forth proliferations which become thallus blades, similar in all respects to the young plants produced from spores. Nine such vegetatively reproduced fronds were found upon a piece of old stipe 5 cm. long.

With reference to plates 21-24 appended to this paper, figs. 3 and 4 represent stages in the development of the plant before the papillae have begun to appear. Fig. 5 shows a small cystocarpic plant, thickly covered with papillae. Fig. 6 shows a segment of a similar frond, on a larger scale.

Proceeding to the internal structure of the thallus, fig. 8 represents a longitudinal section perpendicular to the surface of

the blade. There is a central area, consisting of long, narrow, coarsely granular cells, arranged in series to form filaments. These filaments run in a generally parallel direction with reference to the surface of the thallus, slightly interlacing and connected among themselves by short cross-branches. They occasionally branch dichotomously. Scattered among them are other long, branching and connected cells, the contents not perceptibly granular but staining deeply with fuchsin, similar to the carpogenous cells of the cystocarp, to be described later.

Outside of this central skein of elongated cells is a region consisting of rather short, linear cells arranged in an irregularly branching formation and tending toward the cortical layer at various angles. Interspersed among these are numerous large, oblong and spheroidal cells of granular content, connected with each other and with the surrounding linear cells by pits. The outer cortical layer originates in medium-sized spheroidal cells from which arise, by a dichotomously branching arrangement, the small oblong cells of the anticlinal rows. These anticlinal rows are very short in the young frond, consisting of but one or two cells. Later, the number of cells increases to four or five, or more, making the outer cortical layer proportionately thicker. Conversely, the larger irregular cells of the inner cortical layer, referred to above, are less numerous in the older fronds and in the stipe, so that there is ultimately but little separation between the central skein of elongated cells and the outer cortex. The chlorophyll and red coloring matter of the plant is resident in the cells of this outer layer.

A cross-section of the thallus shows the cut ends and some of the lateral surface of the nearly perpendicularly arranged cells of the central structure, interspersed with the previously mentioned cells of homogeneous content which stain deeply. Outside of this are the smaller cells in a somewhat reticular arrangement interspersed with large and irregular ones, presenting very much the same appearance that they do in the longitudinal section, as do also the cells of the outer cortical layer. The whole structure has the same character in the mid-rib portion as it does in the flat thallus blade, the only difference being that the central

skein is wider, measuring in a direction perpendicular to the face of the blade, in order to produce the mid-rib-like thickening.

The fruiting proliferations are borne at any point upon the surface of the thallus, generally in such abundance as to appear crowded together. This is especially true of the tetrasporic proliferations, which give to the fronds upon which they grow a plush-like appearance and feeling. The tetrasporic proliferations are easily distinguished from the cystocarpic by their somewhat greater length and smaller diameter. They taper gradually toward the base and toward the more or less bluntly pointed apex. Their length varies from ¾ to 1 millimeter, or more. Their width is, in general, from ¼ to ⅓ millimeters. The internal structure is rather loose, consisting of short cells in the contracted, or neck portion, and larger, longer cells constituting filaments running longitudinally to the apex. The cortical layer is similar to that of the frond, the tetrasporangia themselves being simply differentiated cells of the outer cortical layer, much enlarged, ellipsoidal in shape and irregularly divided by planes oblique to their longitudinal and transverse diameters. They may be clearly seen with a ⅔-inch objective, appearing as dark red bodies among the lighter colored cortical cells of the proliferation. Fig. 7 is a diagrammatic representation of a small thallus lobe, bearing tetrasporic proliferations. Fig. 9 is a drawing from a longitudinal section of a proliferation, showing the tetrasporangia in position, together with a still further enlarged view of the same, free from the proliferation.

The cystocarpic proliferations are somewhat shorter, and considerably thicker than the tetrasporic and lighter in color. They are borne upon separate plants from those which produce the tetraspores. Though the vegetative structure is identical, the cystocarpic plants may readily be recognized by noting the characteristics of the fruiting proliferations with a hand-lens.

In the development of the cystocarp an elevation of the cortical layer of the thallus is first noted, proceeding from a lateral growth of cells from the central structure of the frond. This elevation progresses to the formation of a young cystocarpic proliferation which has, at first, a structure resembling that of

the thallus. As the proliferation lengthens a secondary stage is reached in which a marked differentiation of the cells appears, many of them enlarging and becoming filled with a coarsely granular protoplasm and connecting with each other by pits of relatively large diameter. The next stage is marked by the beginnings of the carpogenic branches, arising from the cells of the inner cortex. From these groups come finally the gonimoblast filaments from which are produced the spores. Fig. 10 is a drawing from a paraffin section, stained with fuchsin, showing parts of various carpogenic cells, with groups of spores separated by partitions of vegetative cells.

The carpogenic branch consists, primarily, of three large, irregularly oblong cells, connected at their smaller ends by pits. The larger ends are broad, with a tendency to form more or less distinct lobes. The series is continued by two smaller, curved, rather narrow cells, connected by pits with each other and with one of the larger cells above mentioned (cf. fig. 11). Joined to the last small curved cell by a pit from its base, is a minute triangular cell, the apex being prolonged into a filiform extension, which, after making a spiral turn, joins at right angles a lateral off-shoot from the base of the trichophore (cf. fig. 11). The trichophore is of comparatively large size in its lower portion, gradually contracting above to form the trichogyne. The latter makes its way through the cells of the cortical layer and the gelatinous coat of the proliferation, beyond which it is but slightly prolonged.

After fertilization, presumably, though this process has not as yet been observed by the writer, the trichophore sends out a filament from its basal portion, upon the side opposite the extension which connects with the small triangular cell above mentioned (cf. fig. 11).

This filament was observed in various stages of development, varying from a mere protuberance upon the side of the trichophore, up to and exceeding the relative length represented in fig. 11. A fusion of this tube from the procarp with one of the large carpogenous cells was noted in several instances, yet, owing to the fact that the cells became more or less detached from each

other, and their relative positions altered, in the crushed preparations employed, it has not been possible, so far, to determine with which one of the carpogenous group this fusion takes place. The indications, however, appear to denote a union with the basal cell.

Furthermore, a fusion of the three large carpogenous cells occurs as represented in fig. 12. Whether this fusion takes place as a preliminary to the formation of gonimoblast filaments, or whether it only happens in the absence of fertilization, as Schmitz says is the case in Callymenieae (1897, p. 355), we are unable, as yet, to say. At all events, large irregular, usually tripartite cells finally arise from the carpogenous group, from which proceed a profusion of filaments (cf. fig. 13). These large irregular cells appear to have their origin in the fusion of the three cells above referred to, though instances were not wanting in which but one of the group seemed to be responsible for their formation. From the fact that the instances in which an unmistakable fusion of the three large carpogenous cells occurred were very numerous it is probable that the former is the case, and, also, that the gonimoblast filaments arise from these. As the final determination of this point, however, is not vital to this paper, its further investigation has been deferred.

The gonimoblast filaments, arising from the carpogenous groups, run inward for the most part, toward the center of the proliferation. The carpospores were seen to be connected in some cases with filaments, while in others they were gathered together in groups, without apparent connection with each other or with filaments. As these carpospores finally become very numerous in the proliferation and as they are packed closely together in groups on account of being developed from a number of carpogenic branches acting independently, they push the vegetative cells together, forming partitions, as it were, between the various aggregations. The so-called compound cystocarp, characteristic of Gigartinaceae, is thus produced (cf. fig. 14). The development of the spore groups is principally inwards, as just stated, and there is little or no compression of the vegetative cells surrounding the fruit body, to form a filamentous coat. Another Gigartinaceous feature is seen in the not infrequent branching of

the cystocarpic proliferation, and the formation of fruit bodies in each division.

In the figure last referred to, the manner of freeing the spores is also shown. In the course of its development the wall of the fruiting proliferation becomes distended more upon one side than upon the other. Upon this distended side the cortex is thinner, especially toward the apex of the proliferation, where it consists, ordinarily, of but the outer cortical layer with one or two rows of small cells. This thin portion of the wall of the proliferation finally breaks down, allowing the escape of the spores. No carpostomes are present.

In conclusion, it would appear that *Erythrophyllum delesserioides,* by virtue of the character of its fruiting proliferations, its so-called compound cystocarp with spore-groups separated from each other by partitions of vegetative cells, and by virtue of its vegetative structure, belongs among the Gigartinaceae, as Agardh at first stated. Furthermore, the character of the carpogenic branch and the method of spore formation only strengthens the belief, which the vegetative structure at once suggests, that its place, according to the present classification, is very near to the Callymenieae. In fact, it would seem that Schmitz's description of the carpogenic branch and the manner of spore production in Callophyllis would apply almost equally well to *Erythrophyllum delesserioides.*

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EXPLANATION OF PLATES.

Figures from freehand drawings by the writer.

PLATE 21.

Fig. 1.—Drawn from Setchell's tracing of Agardh's type specimen.

Fig. 2.—From a fragment of an old plant of *Erythrophyllum delesserioides*, similar to Agardh's later specimens, assigned by him to *Polyneura californica*.

Fig. 3.—From a specimen in the University of California herbarium, showing a younger stage in the vegetative development of *Erythrophyllum delesserioides*, before the formation of papillae.

Figs. 1, 2, 3, natural size.

Fig. 1.

Fig. 2.

Fig. 3.

PLATE 22.

Fig. 4.—Showing a plant which has reached full vegetative development, but as yet without papillae.

Fig. 5.—From a still older, comparatively simple specimen of the same, showing the development of papillae in the cystocarpic plant. The tetrasporic fronds are similar in appearance.

Figs. 4, 5, reduced ⅓.

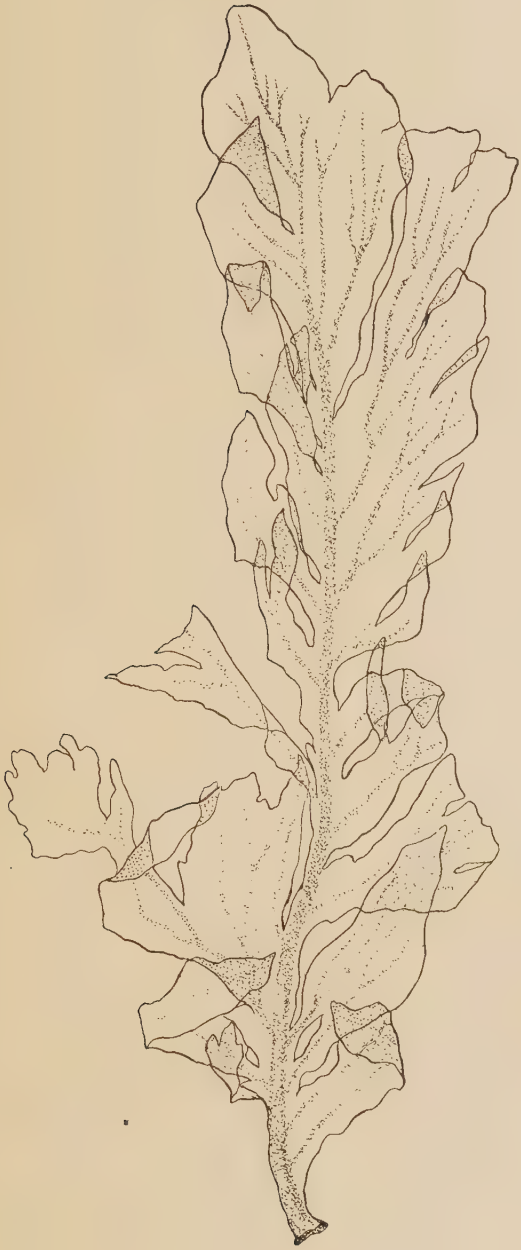

Fig. 4.

Fig. 5.

PLATE 23.

Fig. 6.—Segment of the above, enlarged.

Fig. 7.—Drawn from a paraffin cross-section of a very small tetrasporic frond, showing papillae in longitudinal section. Enlarged 10 times. Diagrammatic.

Fig. 8.—From a frozen longitudinal section, representing the structure of the vegetative frond with its central skein of interlaced filaments, among which is one of the larger cells which stain deeply; the inner cortex, with its large granular and short rhizoidal cells; and the outer cortical layer, with its rows of anticlinal cells.

Fig. 9.—From a longitudinal section of a paraffin preparation of the tetrasporic proliferation, showing the tetrasporangia in position in the outer cortical layer. Upon the left, the tetrasporangia are shown enlarged.

Fig. 6, enlarged ⅓. Fig. 7, enlarged 10 times.

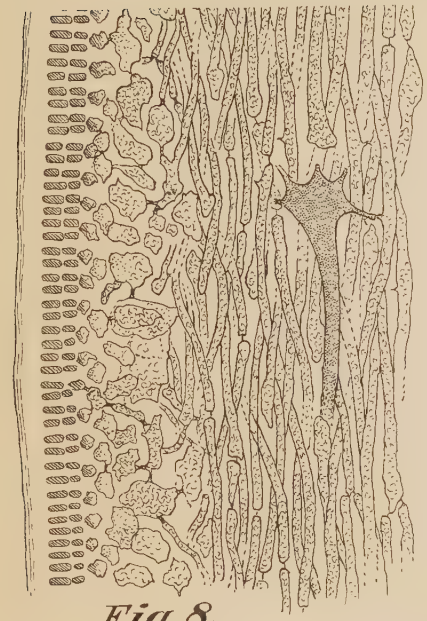

Fig. 8.

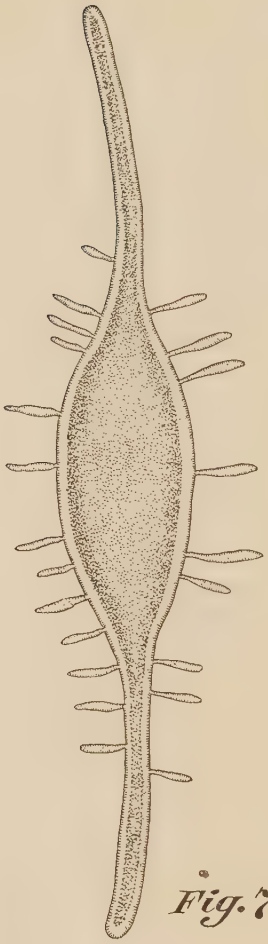

Fig. 7.

Fig. 9.

Fig. 6.

PLATE 24.

Fig. 10.—From a longitudinal section of a paraffin preparation of the cystocarpic proliferation, showing parts of carpogenous groups near the cortex of one side and early stages of spore groups.

Fig. 11.—Carpogenic branch with trichophore, showing conjugating tube which is produced in case of fertilization. This is a composite drawing made from numerous sketches of crushed material, stained with fuchsin. Though more or less apparent variation was observed in the carpogenic group, these are the forms of the individual cells occurring most constantly, and may, therefore, be regarded as typical.

Fig. 12.—Showing fusion of large cells of carpogenic branch, analogous to that which takes place, according to Schmitz, in Callophyllis, in the absence of fertilization. From crushed preparation, stained with fuchsin.

Fig. 13.—From a similar preparation, showing the tripartite body which results presumably from a later stage of the fusion depicted in Fig. 12. The old trichophore, and what seems to be the conjugating tube, are seen above.

Fig. 14.—Drawn from a longitudinal section of a paraffin preparation of the mature cystocarp, showing the dense masses of spores, separated by partitions of vegetative cells. The outer cortical layer is seen breaking away to allow the escape of the carpospores.

Fig. 10.

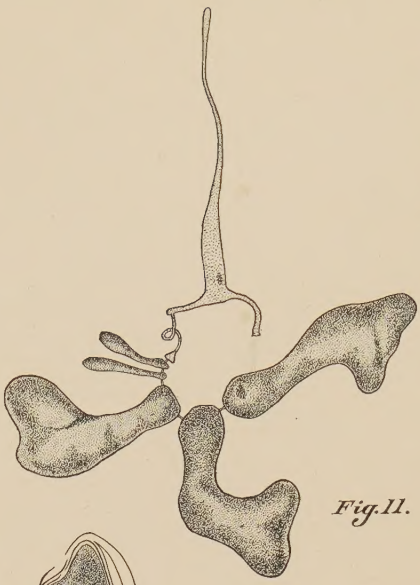

Fig. 11.

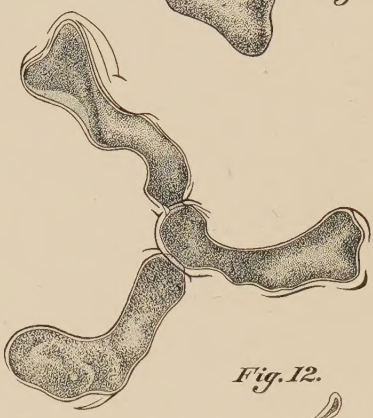

Fig. 12.

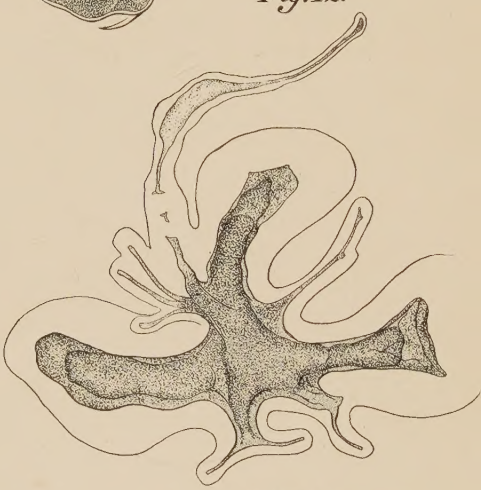

Fig. 13.

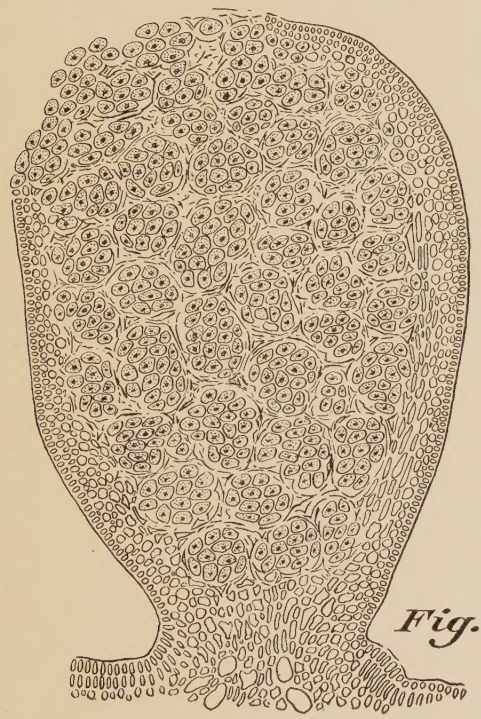

Fig. 14.

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